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Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*)

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Abstract Social foragers can benefit from others' success by joining and sharing their food discoveries. In a producer-scrounger (PS) system, foragers can either search for food themselves (play producer) or search for joining opportunities (play scrounger), but not both at the same time. Empirical evidence is accumulating to show that the joining decision of ground-feeding birds like nutmeg mannikins (*Lonchura punctulata*) can be modeled by a PS game. However some predictions remain to be tested. For instance, foragers are predicted to increase their use of the scrounger tactic as group size increases. Also, one consequence of the incompatibility between producer and scrounger tactics is that the per capita searching efficiency should decrease as the use of scrounger increases. I tested these predictions in an indoor aviary using four flocks of nutmeg mannikins. I manipulated the stable equilibrium frequency (SEF) of the scrounger tactic by varying group size and the finder's share. As predicted by PS games, birds increased their use of scrounger as group size increased. Also, the per capita interval between patch discoveries increased and the per capita finding rate decreased as conditions called for a higher SEF of scrounger. I discuss why the decreased searching efficiency observed likely follows from the incompatibility between producer and scrounger tactics rather than from artifacts of the conditions used or from any form of interference.

Keywords Group size · Nutmeg mannikins · Producer-scrounger · Searching efficiency · Social foraging

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Introduction

Solitary foragers must search for food themselves. Group foragers can also search for their food but in addition they can search for others that have found food and join them. The economic consequences of the decision to join others' discoveries have been modeled so far in two ways that differ in the degree of compatibility that is assumed between the two search modes: the information-sharing (IS) and the producer-scrounger (PS) models (see Giraldeau and Beauchamp 1999). IS models assume that foragers can search for both finding and joining opportunities concurrently: search modes are compatible (Clark and Mangel 1984; Ranta et al. 1996, 1998; Ruxton et al. 1995). PS games, on the other hand, assume that foragers search either for finding (play producer) or for joining opportunities (play scrounger) but never both at the same time: search modes are therefore incompatible (Barnard and Sibly 1981; Caraco and Giraldeau 1991; Giraldeau and Caraco 2000; Vickery et al. 1991).

Contrary to IS models, which usually predict a fixed frequency of joining, PS models predict that the frequency of joining is flexible and varies in response to several ecological factors (Giraldeau and Beauchamp 1999; Giraldeau and Caraco 2000). A number of empirical studies using pigeons (*Columba livia*), nutmeg mannikins (*Lonchura punctulata*), zebra finches (*Taeniopygia guttata*) and starlings (*Sturnus vulgaris*) report flexibility in the frequency of joining, suggesting that the PS game likely applies to these ground-feeding birds (Beauchamp 2001a; Coolen et al. 2001; Giraldeau and Lefebvre 1986; Giraldeau and Livoreil 1998; Giraldeau et al. 1994; Koops and Giraldeau 1996). Rate maximizing PS models (Vickery et al. 1991) predict that the stable equilibrium frequency (SEF) of the proportion of scrounger (s) in a foraging group of G individuals is a function of the finder's share (a/F), that portion of a patch containing F indivisible items that goes to the exclusive use of its finder, such that: $s = 1 - \frac{a}{F} - \frac{1}{G}$.

It follows that decreases in the finder's share and increases in group size should both lead to increases in

scrounger frequency (Beauchamp 2001b; Caraco and Giraldeau 1991; Giraldeau and Beauchamp 1999; Giraldeau and Caraco 2000; Vickery et al. 1991). The finder's share has been successfully manipulated in zebra finches (Giraldeau et al. 1990), in nutmeg mannikins (Coolen et al. 2001; Giraldeau et al. 1990; Giraldeau and Livoreil 1998) and in capuchin monkeys (*Cebus apella*, Di Bitetti and Janson 2001) through changes in food distribution. The finder's share is smaller when food items are clumped in a few rich patches. Studies have shown that nutmeg mannikins increase their joining frequency (Giraldeau and Livoreil 1998) and even their allocation to the scrounger tactic (Coolen et al. 2001) as food was more clumped, i.e. with decreasing finder's share, lending further support to the applicability of the PS game to ground feeding granivorous birds. The effect of group size on tactic use, however, has not yet been empirically tested. If a PS game indeed applies to nutmeg mannikins, then birds should also increase their relative use of the scrounger tactic as group size increases.

The incompatibility that is assumed between the producer and the scrounger tactics has important economic implications for social foragers (Giraldeau and Caraco 2000; Giraldeau and Livoreil 1998; Vickery et al. 1991). Because food finding can occur only when playing the producer tactic, an individual engaged in the scrounger tactic does not contribute to the group's searching effort. Therefore, the group searching effort is expected to decline as the scrounger tactic becomes more common within the group. Empirical evidence suggests that nutmeg mannikins forage using distinct and likely incompatible tactics, as assumed by PS games (Coolen et al. 2001). Coolen et al.'s (2001) results suggest that hopping with the head down and with the head up indicates the use of producer and scrounger tactics, respectively. Indeed, they found that the more birds hopped with the head down, the more they found food patches, and the more they hopped with the head up, the more they joined others' discoveries. Moreover, birds' relative use of hops with the head up increased as changes in food distribution called for an increased use of scrounger. Finally, birds ceased hopping with the head up in conditions where payoffs to scrounger equaled zero. If nutmeg mannikins do forage according to a PS game, then their per capita searching efficiency should decrease as conditions, such as increased group size, call for a higher SEF of scrounger.

The objectives of this study were thus twofold. Firstly, I tested whether flocks of nutmeg mannikins increased their use of the scrounger tactic with increasing group size. Secondly, if as predicted by PS games the birds responded to increasing group size by increasing their use of scrounger, then I tested whether the per capita searching efficiency declined, that is whether the per capita interval between successive patch discoveries increased and the per capita finding rate decreased, as scrounger use increased. Searching here refers to inter-patch search, not to intra-patch search. I tested this second prediction by also

manipulating food distribution in order to increase the confidence that a decline in per capita searching efficiency was directly attributable to the use of the scrounger tactic rather than to artifacts of group size. I tested these predictions by submitting four flocks of nutmeg mannikin individuals to three treatments that involved two group sizes and two finder's shares (a/F): (Small G , Large a/F), (Large G , Large a/F) and (Large G , Small a/F).

Methods

General

I identified 24 commercially purchased wild caught nutmeg mannikins with colored leg bands and small acrylic paint marks on the head and tail. The species is sexually monomorphic and so gender could not be determined easily. I randomly grouped these social, granivorous birds into four flocks and maintained them on a 12:12 h light:dark cycle at temperatures of 24–25 °C with ad libitum access to water at all times. Birds in each flock were of a similar age class. Outside of experimental periods animals were housed together in a 214×61×92 cm holding cage and had ad libitum access to a mixture of vitamin-supplemented white, red, golden and Siberian millet as well as canary seed.

The aim of the study was not to compare the effects of group size and finder's share on searching efficiency but rather to assess the effect of increased scrounger use, via increased group size and decreased finder's share, on searching efficiency. I varied group size (Small G , Large G) and food distribution (Large a/F , Small a/F) using three experimental conditions in total (Table 1). Each flock received the three conditions in an order that was balanced from flock to flock. Which birds of the large group of six would compose the small group of three was pre-determined randomly for each flock. The effect of group size was studied by comparing (Small G , Large a/F) and (Large G , Large a/F) conditions. For the sake of convenience, those two conditions are heretofore referred to as Small G and Large G conditions, respectively. The effect of food distribution was studied by comparing (Large G , Large a/F) and (Large G , Small a/F) conditions. From now on, these two conditions will be referred to as Large finder's share and Small finder's share conditions, respectively. Consequently, the condition (Large G , Large a/F) will be referred to as Large G when looking at the effect of group size and as Large finder's share when looking at the effect of food distribution. In the Small G condition, flocks of three birds foraged on a dispersed food distribution where ten food patches, each containing five seeds, were randomly chosen among 99 wells. In the Large G /Large finder's share condition, flocks of six birds foraged on a dispersed food distribution where 20 food patches, each containing five seeds, were randomly chosen among 198 wells. In the Small finder's share condition, flocks of six birds foraged on a clumped food distribution where ten food patches, each containing ten seeds, were randomly chosen among 198 wells.

Experiments were conducted in a 3.50×1.65×2.40 m indoor aviary. Birds foraged on a plywood grid into which wells were drilled at a mean (\pm SE) of 10.16 (\pm 0.07) cm intervals between center points. Wells had a 1.32 \pm 0.02 cm diameter and were 0.83 \pm 0.01 cm deep. Flocks of three birds were presented with a 1.03×1.32 m grid that contained 99 wells whereas flocks of six birds were given a 2.06×1.32 m grid that contained 198 wells. Doubling the foraging area when group size doubled kept the available grid area per bird as well as the number of wells per bird constant across conditions, at 0.23 m²/bird and 33 wells/bird, respectively. The grid rested 75 cm above the floor at a seated experimenter's eye level.

Each flock was placed in the aviary for 2 days to become familiar with the experimental environment. Food was removed after dawn on the second day and all following days. The first training session started 15–16 h after food removal on the morning

Table 1 Characteristics of the three conditions given to each flock of nutmeg mannikins (*Lonchura punctulata*)

Group size	Small <i>G</i> 3	Large <i>G</i> /large finder's share 6	Small finder's share 6
No. of patches/No. of wells	10/99	20/198	10/198
No. of seeds per patch	5	5	10
Total no. of seeds	50	100	100
Foraging area	1.36 m ²	2.72 m ²	2.72 m ²

of the third day. Birds were then trained at a rate of four training sessions per day for 2 days in one condition and tested in this condition at a rate of four trials per day for the next 3 days. The training and testing procedure was repeated for each condition. The order of presentation of conditions was balanced from flock to flock. Training sessions as well as trials started at 0930 hours and occurred at 15-min intervals. A different focal bird was observed on each trial. A trial started when the first bird landed on the grid and ended after 5 min or when the focal bird had left the grid for more than a minute, whichever occurred first. At the end of testing the birds were returned to the colony's holding cages, a new flock was placed in the aviary and the procedure repeated.

Estimating the effect of group size

On tactic use

I followed Coolen et al.'s (2001) behavioral definitions of producer and scrounger tactics: hopping with the head down and with the head up, respectively. I observed a randomly selected focal bird directly through a one-way mirror while it foraged within the flock. I recorded behavior occurrences during trials directly onto a 386 PC laptop using the Noldus Observer software and noted the following events: "head up" when the line between the eyes and the nostrils was at or above the horizontal (otherwise it was "head down"), "stationary" when a bird marked a pause in its current activity and remained in the same location for 0.5 s or more, "hopping" when it jumped forward. Each hop in a bout of hopping was recorded. A bird "found" when it fed from an unoccupied patch and "joined" when other birds were currently feeding at the same patch or had just fed from that patch. I also noted whenever the focal bird flew to the cover and when it returned to the foraging grid.

I included in the analysis only the data for the three birds of each flock that were present in both Small *G* and Large *G* conditions. The remaining three birds of the Large *G* condition were considered as a core flock and as such were excluded from the analysis. I estimated for each bird and for each trial the relative allocation to the scrounger tactic by calculating the relative investment in hops with the head up as the proportion of all hops devoted to that head position. I then calculated a mean proportion from the repeated observations for each bird and for each condition. I did the same for the proportion of joining events, defined as the proportion of all feeding events that resulted from joining. I compared these proportions using repeated measures ANOVAs (ANOVAR), with each flock as the blocking factor. I used arcsine square-root transformed values when data were not normally distributed and ranked values when arcsine square-root transformation failed to normalize data (Potvin and Roff 1993). The assumptions of homogeneity of variances and of sphericity were met. All statistical analyses were performed using SPSS version 10.0 for PC.

On searching efficiency

For the collection of data on searching efficiency, a video-camera placed outside the aviary, at 1.35 m above the level of the foraging grid, recorded the foraging flock from above through a one-way mirror. Two videos were recorded per day of testing, but only one videotaped trial was randomly chosen per day of testing and used in data analyses. Data were recorded from these videotapes using Noldus Observer. I noted whenever a food patch was discovered, regardless of which flock member discovered it. I also noted con-

tinuously the number of birds that were present on the grid. Searching efficiency was measured as per capita interval between successive patch discoveries and per capita finding rate. Those two measures of searching efficiency are not the corollary of one another: the data points used differ substantially as described below.

I calculated the per capita interval between patch discoveries, regardless of the number of birds that were present on the grid. An interval corresponded to the time elapsed between the beginning of one patch discovery and the beginning of the next, including feeding time at the patch. For the analysis, I excluded those intervals during which one or more birds flew away from the grid, as such departures lead to momentary increases in vigilance (Roberts 1995) that could spuriously increase the time needed to find a food patch. However I did not exclude those intervals during which one or more birds landed on the grid because, although Roberts (1995) showed that birds also respond to increases in group size by momentarily increasing their vigilance, this increase is much smaller than the one following birds' departures. Also, most of the increases in group size were attributable to the sequential landing of flock members at the beginning of the trial. The depletion in the number of patches remaining as a trial progressed altered the probability that any one well contained food over time. I used the ten intervals between all patch discoveries (1, 2, 3... 10) to calculate the mean per capita finding interval for each sequential discovery in the treatment with small group size. However, to control for the fact that trials in the large group size condition offered double the number of food patches of those in the small group size condition at the onset, I used only the ten intervals for every other food discovery (1, 3, 5... 19) in trials with large group size to calculate the per capita finding interval for successive discoveries. In this way, the intervals for both treatments relate to patch discoveries that correspond to the same probabilities that a well contains food. I thus estimated the per capita interval for each food patch discovery by calculating the interval between its time of occurrence and the time of occurrence of the previous one, and multiplying it by the group size, i.e. by three or six depending on the condition. I then averaged the per capita finding intervals for each flock and compared the means using paired *t*-tests.

I also calculated the per capita finding rate. Because this measure did not allow me to exclude specifically the cases where group size changed, I restricted my analysis to bouts of trials during which all birds in the group were present on the grid. Doing so provides a conservative measure of searching efficiency that truly compares per capita searching efficiency of birds in groups of three versus in groups of six. I thus measured the time (in seconds) that elapsed between the arrival of the last bird on the grid and the last patch discovery that occurred before one or more birds left the grid, and tallied the number of patch discoveries that occurred during that bout. I then divided the number of patch discoveries by the duration of that bout and multiplied by 60 in order to obtain the corporate finding rate for a standard minute of foraging. The per capita finding rate is the corporate finding rate divided by the group size. I averaged those per capita finding rates obtained over the 3 days of testing for each flock and compared the rates using paired *t*-tests.

Estimating the effect of finder's share

On tactic use

The procedure for data collection and statistical analysis was similar to the one used for estimating the effect of group size, except

that I included the data for all six birds of a flock in the analysis because the same six birds were used in both Small and Large finder's share conditions.

On searching efficiency

In order to keep the probability that a well contained seeds constant in comparisons across conditions, I collected data only once ten food patches remained on the grid in both Small and Large finder's share conditions. All other methods for data collection and statistical analyses used to estimate the effect of food distribution on searching efficiency were similar to those used to estimate the effect of group size.

Results

General results

Birds spent a mean±SE time of 112.2±5.9, 128.3±6.4, and 103.3±4.9 s on the foraging grid in the Small G, Large G/Large finder's share and Small finder's share conditions, respectively. Birds did not alter their percent time spent feeding when group size varied (mean±SE; Small G: 22.28±1.31; Large G: 20.47±2.07; ANOVAR: $F_{1,8}=0.524$, $P=0.490$). When food clumpiness increased, however, birds significantly increased the percent time they spent feeding (Large finder's share: 20.09±1.66; Small finder's share: 27.21±2.04; ANOVAR: $F_{1,20}=7.182$, $P<0.02$). However, when excluding from the analysis the four individuals that used the head up in more than 65% of their hops and obtained all of their food through joining in the Small finder's share condition, birds no longer varied in their time spent feeding when food distribution varied, at least not significantly so (Large finder's share: 20.64±1.92 s; Small finder's share: 25.43±2.19 s; ANOVAR: $F_{1,16}=2.428$, $P=0.139$). During a trial, flocks exploited 9.15±0.25/10 patches in the Small G condition, 18.62±0.25/20 patches in the Large G/Large finder's share condition and 9.67±0.26/10 patches in the Small finder's share condition.

Estimating the effect of group size

On tactic use

Birds increased their use of scrounger with increasing group size, as predicted by PS games. The proportion of hops involving a head up increased (ANOVAR: $F_{1,8}=7.12$, $P<0.03$; Fig. 1a) and, as a result, the proportion of feeding events resulting from joining also increased (ANOVAR: $F_{1,8}=7.98$, $P<0.03$; Fig. 1b), when group size increased from three to six.

On searching efficiency

The mean per capita interval between patch discoveries was higher in groups of six than in groups of three birds (paired t -test: $t_3=-7.03$, $P<0.006$; Fig. 2a), suggesting

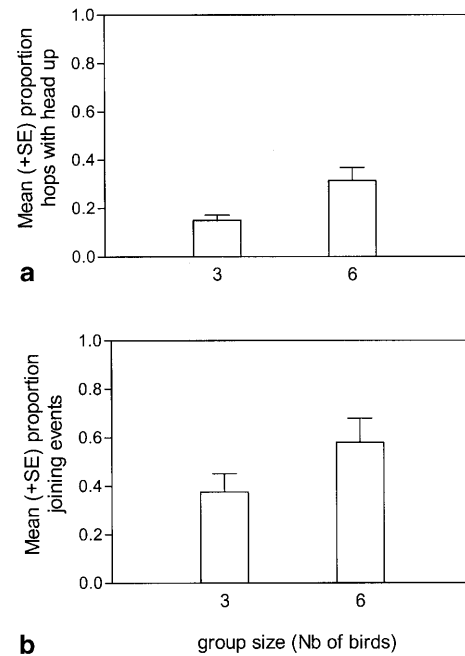


Fig. 1 Effect of group size in nutmeg mannikins (*Lonchura punctulata*) on the mean proportion of hops involving a head up (a) and the mean proportion of feeding events resulting from joining (b)

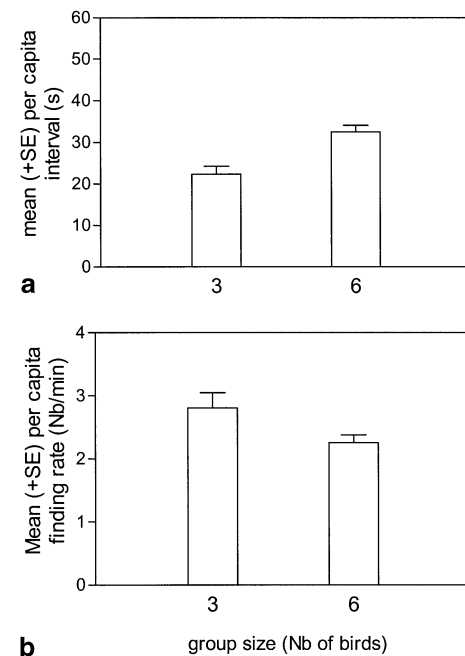


Fig. 2 Effect of group size on the mean per capita interval between patch findings (a) and the mean per capita finding rate (b)

that searching efficiency declined with increasing group size. Moreover, the mean per capita finding rate significantly decreased when group size increased from three to six (paired t -test: $t_3=4.10$, $P<0.03$; Fig. 2b), suggesting also that searching efficiency declined with increasing group size.

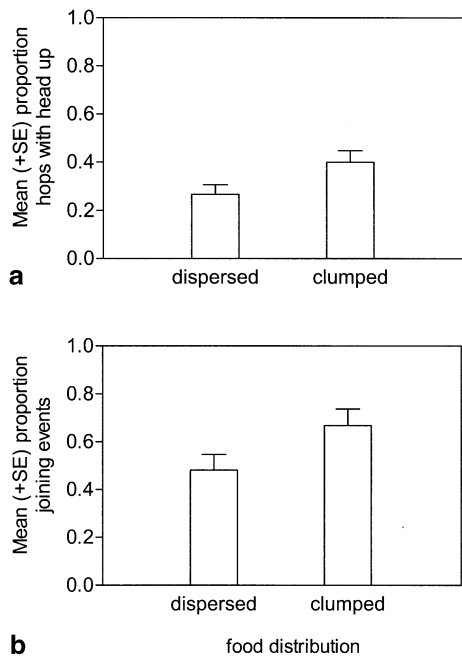


Fig. 3 Effect of food distribution on the mean proportion of hops involving a head up (a) and the mean proportion of feeding events resulting from joining (b)

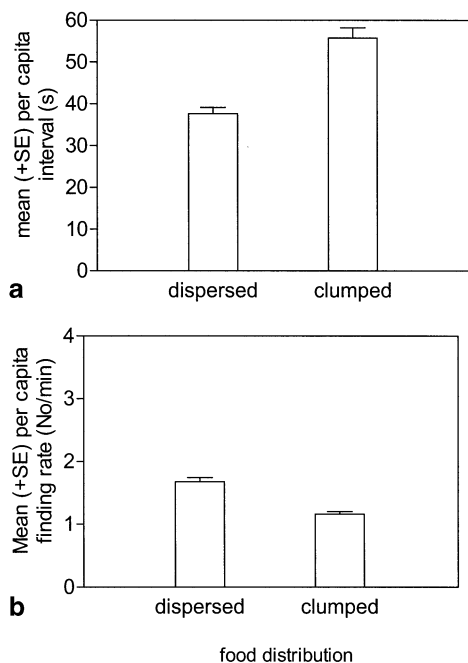


Fig. 4 Effect of food distribution on the mean per capita interval between patch findings (a) and the mean per capita finding rate (b)

Estimating the effect of finder's share

On tactic use

Birds increased their relative use of the scrounger tactic when the finder's share decreased. The proportion of hops associated with head up increased (ANOVAR:

$F_{1,20}=16.90$, $P<0.001$; Fig. 3a) and, as a result, the proportion of feeding events resulting from joining increased (ANOVAR: $F_{1,20}=9.49$, $P<0.006$; Fig. 3b) when the finder's share decreased.

On searching efficiency

The mean per capita interval between patch discoveries was significantly higher when the finder's share was small than when it was large (paired t -test: $t_3=-6.94$, $P<0.007$; Fig. 4a). Moreover, the mean per capita finding rate significantly decreased from the Large to the Small finder's share condition (paired t -test: $t_3=12.05$, $P<0.002$; Fig. 4b).

Discussion

This study adds to the current empirical evidence that ground-feeding birds like nutmeg mannikins do forage according to a PS game: birds varied their use of the scrounger tactic in response to group size and to the finder's share, in the direction predicted by PS games (Beauchamp 2001b; Giraldeau and Caraco 2000; Vickery et al. 1991). An increased use of scrounger with decreasing finder's share has already been reported in previous studies (Coolen et al. 2001; Giraldeau and Livoreil 1998). However, this study provides the first empirical evidence that group size is an ecological determinant of the SEF of scrounger. Note that not only the proportion of joining increased with group size, but also the proportion of hops with the head up, a behavior reported to indicate the use of the scrounger tactic (Coolen et al. 2001). Also, as expected if producer and scrounger tactics are incompatible search modes, per capita searching efficiency declined as conditions called for a higher SEF of scrounger. Indeed the per capita interval between patch discoveries increased and the per capita finding rate decreased in parallel to increased scrounger use, and did so whether scrounger use was manipulated through changes in group size or finder's share (by way of food distribution). This study therefore supports the incompatibility assumed by PS games and reported in nutmeg mannikins (Coolen et al. 2001).

Studies manipulating group size report decreases of per capita searching efficiency that could result from any form of interference (Ekman and Rosander 1987; Ranta and Juvonen 1993), such as an increase in aggression (house sparrow, *Passer domesticus*, Johnson et al. 2001; Alaskan moose, *Alces alces gigas*, Molvar and Bowyer 1994) and in patch revisit rate (greenfinches, *Carduelis chloris*, Hake and Ekman 1988), or individuals may simply hinder each others' movements, as group size increases. In all those studies however, an increase in group size also corresponded to an increase in group density. The decreased searching efficiency reported in those studies is thus more likely due to an increased density of foragers (pteromalid parasitoid, *Cheirropachus*

quadrum, Lozano et al. 1997; blue crab, *Callinectes sapidus*, Clark et al. 2000) than to mere number. None of these forms of interference is likely to have played a role here. In fact nutmeg mannikins can forage and share food without visible aggression (Giraldeau et al. 1990). Moreover I controlled experimentally for group density by increasing foraging area along with group size, so as to keep the available grid area per bird constant. It could be argued that the flock's density increased as scrounger use increased (Barta et al. 1997; Flynn 1998; Flynn and Giraldeau 2001), but this is unlikely to be the case here. Indeed, also using nutmeg mannikins and a similar set up where flocks of birds searched for food patches on a grid, Flynn (1998) reports that group density increased by 18% when scrounger use increased by 356%. Given that scrounger use here varied by 52.6% and 38.8% with changes in group size and finder's share, respectively, the changes in group density across conditions are likely negligible. Increasing foraging area along with group size also kept the number of wells per bird constant across conditions. As a result, for comparisons of searching efficiency each well had the same probability of containing food whether group size was three or six. In addition, I controlled statistically for any difference in the probability that a well contained food. When comparing the per capita intervals between successive patch discoveries, I compared only patch discoveries that corresponded to similar probabilities of containing food across conditions. Similarly, when comparing the per capita finding rates, I used only bouts of trials in which the range of probabilities was the same across conditions. I argue that the experimental and statistical procedures used likely controlled for the degree of search interference that would normally be associated with increasing group size (Hake and Ekman 1988). It is conceivable that the degree of overlap between the flock members' search areas even decreased with group size, because fewer birds actually searched for food at any one time given the increased allocation to the scrounger tactic.

Food distribution bears potential artifacts that could also be responsible for a decrease in per capita searching efficiency aside from the increased use of the scrounger tactic itself. For instance, in the comparison involving different food distributions, data from the Large finder's share condition was collected only once the birds had already fed from ten patches. Arguably this extra feeding could have lowered the birds' hunger and searching efficiency (Morgan 1988). However, I observed that these birds had the highest searching efficiency and so the effect cannot be explained easily by extra feeding.

Any increase in the time spent feeding may reduce the time spent searching and thereby cause a spurious decrease in per capita searching efficiency. The diameter of food wells allowed only one bird to peck at a seed at a time, forcing birds that shared a patch to peck sequentially. The time needed to collect a seed and thus the time spent feeding in a trial may then have increased as the number of potential foragers feeding from the same

patch increased. The number of potential foragers feeding from the same patch likely increased with group size, as suggested by the increased proportion of joining events. However, birds did not spend more of their time feeding as group size increased and so it is unlikely that the decreased per capita searching efficiency observed in the Large *G* condition was caused by increased feeding time. The time spent feeding may have been altered in conditions of varying finder's share because patch size varied from five to ten seeds. It is conceivable that when the distribution of seeds involved larger patches the birds spent more time feeding, and thereby less time searching. Even though birds increased their time spent feeding as the finder's share decreased, the increase in feeding time was slight and likely translated only in a slight, if any, decrease in searching efficiency. Moreover the increase was no longer significant when discarding individuals that participated little in group searching effort and not at all to its success.

For all these reasons, it seems unlikely that the conditions I used produced artifacts leading to a spurious decrease in searching efficiency. If such artifacts existed, however, their effect would have been small and could not have caused a decline in per capita searching efficiency the size of the one reported here. Moreover, the two different methods used to manipulate scrounger use both lead to a decrease in per capita searching efficiency. This strongly suggests that the decrease in per capita searching efficiency observed was attributable to the incompatibility that lies between producer and scrounger tactics rather than to artifacts of food distribution or to any form of interference. It has long been known that social foraging reduces searching efficiency of the group members by way of interference and aggressive kleptoparasitism. Yet this study contributes the first empirical evidence of an additional cost associated with the use of the scrounger foraging tactic (Giraldeau and Caraco 2000; Vickery et al. 1991).

The results reported here involve foraging nutmeg mannikins but they more generally apply to any species for which searching for a resource or for successful group members to join represents incompatible search modes. The incompatibility described here is behavioral but it could also be cognitive. Individuals may not be able to process two types of information at the same time and attention may be divided between the two (Dukas and Kamil 2000). Likewise, incompatibility may arise through individual specialization to either tactic when food searching requires the learning of a specific task (Flynn and Giraldeau 2001; Giraldeau et al. 1994). Also, incompatibility may not be fixed for a species but depend upon the situation. For instance, searching for a given resource may require a greater deal of attention when the resource is blended with the background than when it is conspicuous and incompatibility likely arises as the required level of attention to the task increases (Dukas and Kamil 2000; Lawrence 1985). Consequently, the costs identified here likely extend to any situation where incompatibility arises. Future studies need to

identify such situations and to confirm that incompatibility indeed results in reduced per capita searching efficiency.

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